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1 Non-native species in the vascular flora of highlands and mountains of

2 Iceland

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6

7 Abstract

8 The highlands and mountains of Iceland (defined here as areas located above 400 m a.s.l) are one
9 of the largest remaining wilderness areas in Europe. The present study provides the first
10 comprehensive and up-to-date data on non-native plant species from these wilderness areas.

11 Overall, 16 non-native vascular plant species were detected, including 11 casuals and 5
12 naturalised taxa (1 invasive). Results showed that the central highlands are most vulnerable to
13 non-native plant colonisation, while other mountain and highland areas in Iceland seem to be far
14 less impacted by non-native plants. Clear hotspots of alien flora are evident, especially in popular
15 tourist areas in the highlands and mountains such as hot springs, geothermal areas, mountain
16 huts and shelters, as well as main roads and tracks. Temporal trends characterizing non-native
17 plant colonization show that the process is still in its initial phase. This research suggests that
18 human-mediated dispersal is the main driving force increasing the risk of invasion in Icelandic
19 highlands and mountain areas.

20

21 Key words

22 alien flora, Iceland, highland, mountain flora, invasive species, tourism

23

1 Introduction

2 There are conflicting views on the question whether the Arctic should be considered a
3 pristine, virgin environment or whether it has been changed and influenced by human activities
4 (Elven et al. 2011). It seems that if vascular plants are taken into account, the former point of
5 view is more appropriate. Overall, there is no known evidence of human mediated extinction of
6 any Arctic vascular plant species, the total number of naturalised alien plant species is low or
7 negligible in most of the Arctic's phytogeographic regions, and the natural "phytogeographic"
8 pattern is intact in the Arctic (Elven et al. 2011). However, this is not the case in the North
9 Atlantic region of the Arctic that encompasses Greenland and Iceland, where human settlements
10 date back to Medieval times (McGovern 1990). In this region the number of non-native plants is
11 much higher, especially in areas with a long history of human activity (e.g. Wasowicz et al.
12 2013).

13 The highlands and mountains of Iceland (defined here as areas located above 400 m
14 a.s.l), which account for ca. 40% of the country, are some of the most pristine environments of
15 Europe due to their remoteness and harsh climate (Einarsson 1994). The central highlands are
16 considered the largest territories in Europe south of the Arctic Circle that have never been
17 permanently settled by humans (Vésteinsson 1998). Since the retreat of the ice sheet from the
18 last ice age, undisturbed processes of ecological succession have created a variety of unique,
19 natural plant communities that have been found to be one of the key factors in maintaining
20 natural plant distribution patterns in Iceland (Wasowicz et al. 2014). It seems, however, that the
21 combination of increasing anthropogenic pressure and climate change may contribute to
22 significant changes in these fragile ecosystems (Wasowicz et al. 2013).

1 Non-native plant species are one of the main threats to the unique biodiversity in the
2 Icelandic highlands. Alien plant species can significantly impact species richness, survival and
3 productivity of native communities (Gaertner et al. 2009, Pysek et al. 2012a). Furthermore, non-
4 native plant colonization is far more likely to negatively impact native plant and animal richness
5 on islands than on the mainland (Pysek et al. 2012a). Climate change is another risk factor that
6 may seriously affect the flora in the Icelandic highlands by deteriorating habitat conditions for
7 native, cold adapted species (Lassuy and Lewis 2013, Wasowicz 2013) and favouring the spread
8 of alien species, leading to new invasions and range expansion of already naturalised alien taxa
9 (Thuiller et al., 2007).

10 Given these threats to the Icelandic highlands and mountains, the present study aimed to
11 evaluate the impact of non-native plant taxa on the vascular flora of these areas . The objectives
12 of the study were to:

- 13 (1) generate a checklist of alien plant species present in the Icelandic highlands and
14 mountains
- 15 (2) assess their naturalisation status
- 16 (3) define spatial patterns and hotspots of their distribution
- 17 (4) analyse temporal trends in the data.

18 **Materials and methods**

19 *Definitions used*

20 The study focused on non-native plant species as defined by Pysek et al. (2004), which
21 represent taxa whose presence in a given area is due to intentional or unintentional human
22 involvement or which have arrived there without human intervention from an area where they
23 are alien. Non-native species are further subdivided into two categories: casual and naturalised

1 species. Casual species were defined as alien plants that may flourish and even reproduce
2 occasionally outside cultivation in an area, but that eventually die out because they do not form
3 self-sustaining populations, and rely on repeated introductions for their persistence. Naturalised
4 species on the other hand, were defined as alien plants with self-sustaining populations for at
5 least 10 years without direct human intervention (or in spite of human intervention), but rather
6 by recruitment from seed or ramets (tillers, tubers, bulbs, fragments, etc.). Invasive alien species
7 were included under naturalised taxa, and followed Pysek et al.'s (2012 b) definition.

8 *Data origin*

9 Data were obtained from the Icelandic Institute of Natural History. The institute has the
10 largest repository of biodiversity data in Iceland, containing over 500,000 georeferenced
11 records of plant species distribution. Only records of non-native taxa (Wasowicz et al. 2013)
12 were considered for the study. Overall, 9,396 records collected between 1840 and 2014 were
13 examined, including vouchered specimens deposited in AMNH and ICEL herbaria, field
14 observations and literature data records.

15 *Spatial analyses*

16 All georeferenced data from the database were converted into shapefiles using QGIS
17 software. Elevation data were retrieved from digital elevation model of Iceland (20 m per pixel)
18 downloaded from <http://gatt.lmi.is> . Elevation in meters was then assigned to each data point
19 using point sampling tool in QGIS. A database was developed that contained georeferenced
20 species occurrences and elevation data. This database was queried to identify records with an
21 altitude of ≥ 400 m a.s.l. (130 in total; see supplementary materiall).. In order to identify areas
22 with high concentration of non-native species records, a heat map was generated in QGIS using
23 a radius of 5.000 m.

1 *Checklist, temporal trends*

2 A checklist of non-native taxa was developed, summarizing information on taxonomy,
3 time of residence, naturalisation status, biogeographical affinities and a life form (Raunkiaer,
4 1934). Native distribution of alien taxa was recorded at a continent scale. If the taxa were
5 present in two continents, they were included in both totals.

6 The year of first observation for each species record was retrieved from the database and
7 cumulative number of species introduced and number of observations were plotted against time.
8 Curves were plotted in SigmaPlot using locally weighted regression - LOESS (Cleveland 1979),
9 using a sampling proportion of 0.1 and polynomial degree set to 1.

10
11 Results

12 Overall, 16 non-native plant taxa were recorded in the Icelandic highlands and mountain
13 areas between 1840 and 2014 (Table 1). According to the criteria proposed by Pysek et al (2004),
14 11 taxa (69% of total non-native flora) were classified as casual aliens, while 5 taxa (31% of
15 non-native flora) were classified as naturalised. Based on the criteria by Pysek et al. (2012b),
16 only *Lupinus nootkatensis* can be classified as an invasive plant.

17 All non-native vascular plants in the Icelandic highlands and mountain areas belong to 11
18 families and 16 genera. Only two families were represented by more than one genus: *Poaceae*
19 with 5 genera, and *Boraginaceae* with 2 genera. Hemicryptophytes were the most common non-
20 native plants (10 taxa, 62% of total non-native flora), while therophytes were far less common (2
21 taxa, 12%). Geophytes, nano-phanerophytes and phanerophytes only had one taxon each (6%)
22 (Table 1).

23 Evaluation of the geographic origin of non-native taxa showed that 10 taxa were
24 included in the European group of origin, 9 taxa in the Asian group and 6 taxa in the Northern

1 American group (Table 1). Analysis of the geographic distribution of non-native taxa records
2 indicate that they are concentrated mainly within the central highlands (Fig. 1). A closer
3 examination of the pattern of occurrence within the central highlands, revealed that hotspots of
4 non-native plants coincided with disturbed areas related to man made objects such as huts,
5 shelters and roads. In addition, the highland areas around Myvatn Lake were also a hotspot for
6 non-native species. Highland and mountain areas outside the central highlands appeared to be
7 less colonised by non-native plants. For example, the highlands in the Western Fjords (NW
8 Iceland) and in the eastern part of the country seemed to have the fewest non-native plant taxa.
9 The results showed clearly that naturalised species are a lot more frequent and widely
10 distributed than casual aliens (Fig. 2 b,c)

11 The cumulative number of first taxa records was plotted against time to examine
12 temporal trends in alien taxa immigration to the highlands and mountain areas. The analysis
13 showed that the trend recorded for the highlands and mountain areas is very similar to the overall
14 trend of non-native species immigration to Iceland (Fig. 2a). It seems, however, that a steady,
15 linear increase in the number of non-native taxa records started much later in highlands than in
16 Iceland as a whole (Fig 2a). The same pattern is clearly visible when the number of observations
17 of non-native plant taxa is taken into account (Fig.2 b). A clear growth trend is seen in the
18 highlands a few decades after it started in the lowlands or Iceland as a whole. The curve for the
19 highland areas seems to be a lot steeper than the curve plotted for the entire country (Fig. 2b).

20 Discussion

21 Over 300 non-native plant taxa have been recorded in Iceland so far (Wasowicz et al.
22 2013, Wasowicz 2014). The results of the study indicate that only a very small percentage of
23 these alien species is able to reach the highlands and mountain areas. Currently, 95% of non-

1 native taxa recorded in Iceland has yet to be found in the highlands and mountain areas. This
2 suggests that there are still strong environmental factors preventing unlimited spread of non-
3 native plants from lowland areas to the highlands.

4 Climate is one potential factor that explains the low rate of colonization success among
5 non-native plants in the highlands. With very few exceptions, most of the highlands and
6 mountain areas in Iceland have a mean temperature in July less than 10°C (Einarsson 1984), and
7 thus can be treated as Arctic areas based on climatic criteria (Przybylak 2002). These
8 unfavorable conditions with low temperature and very short vegetation period restricts the
9 growth of many species in the Icelandic highlands and mountain areas, including non-native taxa
10 (Wasowicz et al. 2013). Research on the biogeographical patterns of the native Icelandic flora
11 has also shown that climatic factors are crucial in shaping the geographic distribution of native
12 flora (Wasowicz et al. 2014).

13 It is well known that non-native species richness increases with the level of urbanisation
14 and is positively correlated with human population density (McKinney 2001, Holway 2005).
15 From the beginning of the settlement, farms and other centres of human activity in Iceland
16 were located almost exclusively within lowland areas, especially in flooded wetlands
17 (Vésteinsson 1998), where climatic conditions were good enough for agriculture. This pattern of
18 settlement in turn, limited the economic significance of the highlands and mountain areas that
19 were used almost exclusively for sheep grazing until the mid-1960 (Sæþórsdóttir and Saarinen
20 2015). Low rate of human settlement and visitation and almost negligible economic use of these
21 areas, contributed to extremely small propagule pressure thus limiting the spread of non-native
22 plant taxa in the past.

1 The results suggest that only taxa previously naturalised within lowland areas are able to
2 effectively colonise the highlands. All taxa naturalised in highlands and mountain areas have
3 been recorded as naturalised in the lowlands (Wasowicz et al. 2013). Furthermore, most of the
4 casual taxa in the highlands are naturalised in the lowlands (Wasowicz et al. 2013). This shows
5 that colonization of highland environments in Iceland is a “second step” in the process of
6 naturalisation of the species within the country. There is no evidence available so far showing a
7 different direction of naturalisation process (i.e. a species naturalised in highlands and spreading
8 down into lowlands).

9 Comparison of the geographic origin of non-native plant taxa showed that most have an
10 European origin, constituting 66% of all non-native flora in the highlands, and 49.2% of all non-
11 native plants in Iceland (Wasowicz et al. 2013). Also taxa of Asian and Northern American
12 origin scored high in both in the highlands and the country as a whole. In the highlands, non-
13 native plants from Asia accounted for 55% all alien flora, while 33% of them were from North
14 America. The percentage of non-native plants from North America in the Icelandic highlands is
15 significantly greater than that seen for the entire country (8.9%, Wasowicz et al. 2013).. This is
16 due to the fact that several non-native species from Northern America have been deliberately
17 introduced into the highlands, becoming naturalised at a faster rate than other non-native
18 species. Plants such as *Lupinus nootkatensis*, *Deschampsia caespitosa* subsp. *beringensis* and
19 *Salix alaxensis* are good examples of this. Given the high level of environmental matching
20 between their native range and the Icelandic highland areas, these species are most likely to
21 spread quickly and effectively in the highlands. Currently, Alaska lupine (*L. nootkatensis*) is the
22 most widespread and invasive non-native plant in the Icelandic highlands.

1 Most non-native plants are found in the central highlands. Also, fairly accessible highland
2 areas close to Myvatn Lake (North-Eastern Iceland) have been influenced by naturalised alien
3 plant species. The climatic conditions in the north-eastern part of the country allowed human
4 settlement and farming activities above 400 m a.s.l, facilitating the introduction of non-native
5 plants. In contrast, areas located above 400 m a.s.l. in other parts of Iceland (e.g. the Western
6 Fjords and Eastern Fjords) appear to be almost free of non-native plant species. This pattern of
7 spatial occurrence can be explained by human-mediated dispersal. A closer examination of
8 places with very high numbers of non-native species shows that they are mostly found in areas
9 with tourist attractions such as hot springs (e.g. Hveravellir, Laugafell) and areas with
10 geothermal activity (e.g. Reykjahlíð, Námafjall and Krafla volcano), as well as near hiking huts
11 and shelters along the highlands (e.g. Jökullheimar). The road network into the highlands is
12 another source of propagules and is very likely facilitating the spread of non-native plants into
13 these areas. The study seems to confirm that human-mediated dispersal along a road network is
14 one of the most important factors contributing to plant dispersal (von der Lippe et al. 2013).

15 Temporal trends characterising non-native plant colonization show clearly that the
16 process is still in its initial phase. Relatively low number of non-native plant species was
17 recorded in the highland areas when compared to the rich alien flora in the lowlands (Wasowicz
18 et al. 2013). This suggests that further colonisation may occur, especially if climatic constraints
19 are significantly reduced or even removed by climate change, which has been suggested by
20 recent modelling experiments (Wasowicz et al. 2013). A sharp increase in the number of species
21 observations after 1960, may be indicative that construction of the first large hydropower plants
22 in the central highlands in the mid-1960s contributed to an increase alien plant colonisation. The
23 construction of these hydropower plants involved significant improvements in road

1 infrastructure, making some areas more accessible including Landmannalaugar (Sæþórsdóttir
2 and Saarinen 2015).

3 In recent years Arctic wilderness environments have become a major tourist attraction,
4 and the central highlands in Iceland are considered one of the largest remaining wilderness areas
5 in Europe (Sæþórsdóttir and Saarinen 2015). The increase in international visitors coming to
6 Iceland is particularly high, where the number of tourists has grown from 72,600 in 1982 to ca. 1
7 million in 2014 (Sæþórsdóttir and Saarinen 2015). It is estimated that about one third of tourists
8 visit the central highlands (Icelandic Tourist Board 2012). These values suggest that the influx
9 of propagules carried on the clothing, gear and vehicles of visitors to the central highland is
10 likely higher than ever before and will probably continue to grow with increasing tourism.
11 Recent studies in Antarctica and the Arctic have shown that this type of plant propagule transfer
12 should be considered as very important source of propagules of non-native species (Whinam et
13 al. 2005, Lee and Chown 2009, Ware et al. 2011, Chown et al. 2012, Huiskes et al. 2014). The
14 increased transfer of propagules poses a great danger to the unique and fragile environments in
15 the highlands and mountain areas of Iceland. Moreover, this increased propagule pressure will
16 likely contribute to more secondary invasions of existing non-native species through facilitated
17 seed transport along road networks (von der Lippe et al. 2013), as well as through the arrival of
18 new alien species brought by tourists from lowland areas and abroad. An example of this is
19 *Digitaria ischaemum* (*Poaceae*), which seems to be have spread between thermal areas in
20 southern Iceland via the hiking shoes of visitors. Future actions to facilitate travel through the
21 central highlands (e.g. construction of new road tracks or improvement of existing routes), will
22 inevitably increase the number of visitors, leading to a greater inflow of seeds and other plant
23 propagules of non-native taxa and a higher risk of invasion.

1 Conclusions

2 The present research shows that non-native plant species are one of the major threats to
3 preserving pristine environments in the highlands and mountain areas of Iceland. The presence of
4 16 non-native plants was evidenced, of which almost 30% are already naturalised in the
5 highlands and mountain areas. Some of those species (*Lupinus nootkatensis*, *Deschampsia*
6 *caespitosa* subsp. *beringensis* and *Salix alaxensis*) can be considered as invasive (*L.*
7 *nootkatensis*) or potentially invasive given their environmental matching between their native
8 and novel environments. The central highlands are a hotspot of increased colonisation by non-
9 native plant species, and human-mediated dispersal seems to be a major force contributing to the
10 risk of invasion.

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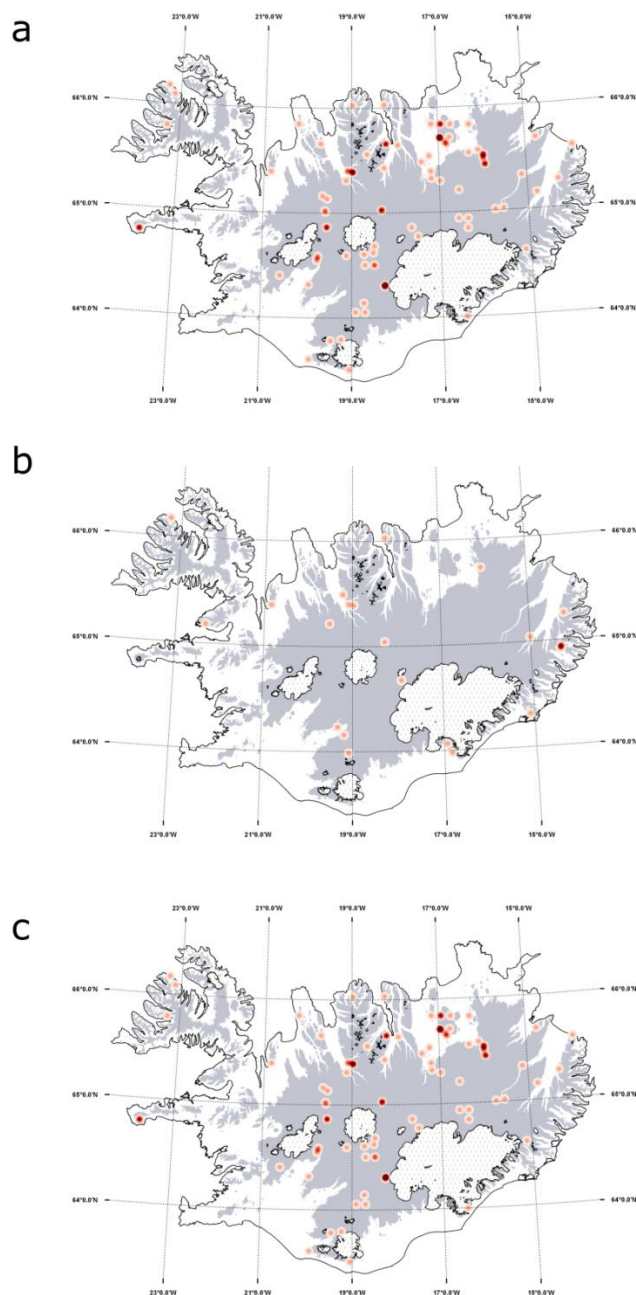
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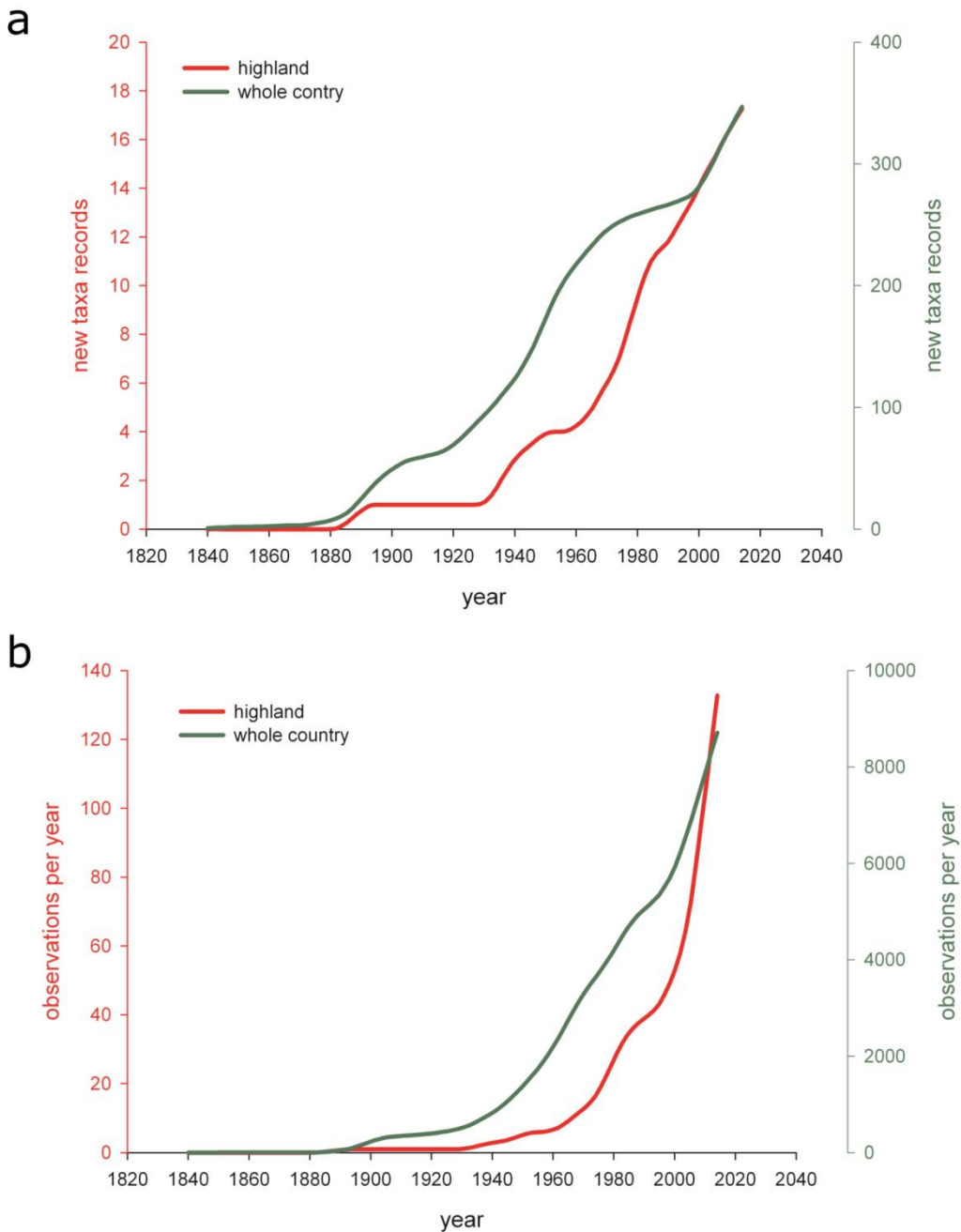
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1
2 **Fig. 1** Heat map showing the clusters of observations of non-native vascular plant species in
3 highland and mountain areas in Iceland. a - all species, b - casual species, c - naturalised species



2

3 **Fig. 2** LOESS curves showing dynamics and temporal trends in non-native flora of highland and
 4 mountain areas of Iceland (1840-2014) - LOESS curves. a - number of species, b - number of
 5 observations. Cumulative numbers were calculated on the basis of *per annum* new taxa
 6 records/observations

Table 1. Checklist of non-native vascular plants in highland and mountain areas of Iceland.

	Species	First record ^a	Last record ^b	Naturalisation status ^c	Life form ^d	Origin ^e	N ^f
1	<i>Alnus viridis</i> (Chaix) DC. ssp. <i>sinuata</i> (Regel) Á.Löve & D.Löve	2005	2005	CAS (NAT)	N	NAm, Asi	2
2	<i>Alopecurus pratensis</i> L.	1963	2011	NAT (NAT)	H	Eu, Asi	15
3	<i>Avenula pubescens</i> (Hudson) Dumort.	1978	1978	CAS (NAT)	H	Eu, Asi	1
4	<i>Claytonia sibirica</i> L.	2004	2004	CAS (CAS)	H	Asi, NAm	1
5	<i>Deschampsia cespitosa</i> (L.) Beauv. ssp. <i>beringensis</i> (Hultén) W.E. Lawr.	1996	2012	NAT (NAT)	H	NAm, Asi	24
6	<i>Lamium amplexicaule</i> L.	1988	1988	CAS (NAT)	T	Eu	1
7	<i>Lappula squarrosa</i> (Retz.) Dumort.	1888	1888	CAS (CAS)	H	Eu, Asi	1
8	<i>Lepidotheca suaveolens</i> (Pursh) Nutt.	1969	1999	CAS (NAT)	T	Eu, NAm, Asi	3
9	<i>Lolium perenne</i> L.	1981	1981	CAS (CAS)	H	Eu, Asi	1
10	<i>Lupinus nootkatensis</i> Donn ex Sims	1980	2014	INV (INV)	H	NAm	44
11	<i>Myosotis scorpioides</i> L.	1978	1980	CAS (NAT)	H	Eu, Asi	2
12	<i>Phleum pratense</i> L.	1935	2010	NAT (NAT)	H	Eu	22
13	<i>Rheum rhabarbarum</i> L.	1996	1996	CAS (CAS)	G	cult	1
14	<i>Salix alaxensis</i> (Andersson) Coville	2011	2011	NAT (NAT)	P	NAm	1
15	<i>Sinapis arvensis</i> L.	1937	1937	CAS (CAS)	T	Eu	1
16	<i>Stellaria graminea</i> L.	1946	2000	CAS(NAT)	H	Eu	7

a) year of the first record is usually taken from databased herbarium collections. In some cases, however, they are based on observations only. This usually refers to taxa that are not present in herbaria collection in Iceland but were listed on the basis of literature reports

b) the data on most recent record are based on both herbarium and observation data

c) established after Pysek et al. (2004): CAS - casual alien species, NAT - naturalised alien species, INV - Invasive alien species. Naturalisation status in the country was given in brackets according to Wasowicz et al. (2013).

d) assigned according to Raukiær (1934) classification: G - geophyte, H - hemicryptophyte T - therophyte N - nano-phanerophytes P - phanerophytes.

e) geographic origin of the species: Eu - Europe, Asi - Asia, NAm - North America, cult - cultivated taxon.

f) total number of examined records